PLATE XLIV.

Fig. 1. *Stachyodes gilchristi*, sp. n., part of branch of. × 8.
2 *a*. *Euplexaura media*, sp. n. Spicules of central trunk.
2 *b*. " " " Spicules of external trunk.
2 *c*. " " " Spicules of polyps.
3 *a*. *Thouarella hicksoni*, sp. n., verruca of. × 45.
3 *b*. " " " apex of verruca of. × 100.
4 *a*. *Muriceides fusca*, sp. n. Spicules of upper part of polyp.
4 *b*. " " " Spicules of lower part of polyp.
4 *c*. " " " Spicules of cœnenchyma.

PLATE XLV.

Fig. 1. *Thouarella hicksoni*, sp. n. Spicules of verruca.
2 *a* & *b*. *Stachyodes gilchristi*, sp. n., sclerites of.
3 *a*. *Psammogorgia pulchra*, sp. n., red spicules of.
3 *b*. " " " yellow spicules of.
4 *a*. *Suberia capensis*, sp. n. Spicules of central trunk.
4 *b*. " " " Spicules of external trunk.
4 *c*. " " " Spicules of polyp.

38. On the Structure of the Skull in Cynodont Reptiles *. By R. BROOM, M.D., D.Sc., C.M.Z.S.

[Received April 10, 1911 : Read May 23, 1911.]

(Plate XLVI.† and Text-figures 168–180.)

Historical and Introductory.

In 1853 the British Museum received from Andrew Bain the first known skulls of fossil reptiles with a mammal-like arrangement of the teeth. These ultimately became the types of *Lycosaurus tigrinus* and *Cynodraco serridens*. In 1858 Sir George Grey presented the skulls which were shortly afterwards described by Owen as *Galesaurus planiceps* and *Cynochampsa laniaria*. The *Galesaurus* skull though crushed was nearly complete, and being so very remarkably mammal-like Owen almost immediately described it in a paper read before the Geological Society on 20th April, 1859.

Although for seventeen years nothing further descriptive of any of the reptiles with a mammal-like dentition was published, it is necessary to briefly consider some of Owen's other work in the interval to clear up a certain confusion of nomenclature. In 1859 Owen gave to the world his famous classification of the fossil reptiles, and though he formed the Order *Anomodontia* for the South African reptiles of the Dicynodont type, he carefully omitted all reference to those reptiles, like *Galesaurus* and *Cynochampsa*, with a mammal-like dentition. When in 1861 he published his 'Palæontology,' feeling compelled to put the remarkable *Galesaurus* somewhere, he made it the type of a "family" of the Anomodontia, calling it the *Cynodontia*, doubtless

* On p. 902 Dr. Broom names a new species, viz. *Cynognathus seeleyi*.—EDITOR.
† For explanation of the Plate see p. 925.

recognising that *Galesaurus* was in some way related to *Dicynodon*, but hesitating to make a new Order on the evidence of a single skull. As he still defined Anomodontia as reptiles with "teeth wanting or limited to a single maxillary pair," it is manifest he did not regard *Galesaurus* as really an Anomodont.

In 1876, when Owen issued his 'Catalogue of the South African Fossil Reptiles' he put all the forms with a mammal-like dentition into a new Order, the *Theriodontia*. In 1903 I showed that Owen's *Theriodontia* is not a natural order, for it included two groups which, though agreeing in having the dentition specialised into incisors, canines, and molars, and possibly the one being ancestral to the other, were yet so dissimilar that they could not be well kept together. The more primitive group, which occurs only in Permian beds, has simple molars, an open Rhynchocephaloid palate, a transpalatine bone, large angular and surangular bones, a single occipital condyle, no acromion process, and apparently a digital formula of 2, 3, 4, 5, 3. The higher group, which is known only from Upper Triassic beds, has usually specialised molars, a secondary palate as in Mammals, no transpalatine, small angular and surangular bones, two occipital condyles, an acromion process, and a digital formula 2, 3, 3, 3, 3. As Cynodontia was the name first applied to animals of the *Galesaurus* type, this title should be retained for the higher group. For the lower forms I proposed the name Therocephalia. The name Theriodontia should be dropped, as only likely to lead to confusion.

Among the new forms described by Owen in his Catalogue is a badly weathered small Cynodont skull somewhat resembling that of *Galesaurus* and named *Nythosaurus larvatus*. In 1887 he described another small but well-preserved skull which he believed to be an additional specimen of *Galesaurus*.

Most of our knowledge of the Cynodonts, however, is due to Seeley, who, as the result of his expedition to South Africa, not only came across the skulls of many new types, principally in the collections of Dr. Kannemeyer, Mr. A. Brown, and the Albany Museum, but for the first time obtained most of the skeleton of some Cynodonts. In one paper issued in 1896 he described a very fine skull with most of the vertebral column, the limb-girdles, and portions of the limbs of a large carnivorous type, which he called *Cynognathus crateronotus*, also a fine skull of an allied form called *Cynognathus platyceps* from the Albany Museum collection. In other papers he described new types of Cynodont reptiles with flat-topped molars. Of these the best known types are *Gomphognathus*, *Diademodon*, and *Trirachodon*. These were regarded by Seeley as belonging to a distinct Order, which he called *Gomphodontia*; but as, apart from the specialisation of the molars, there are no characters of any importance to distinguish the Gomphodonts from the Cynodonts, it seems to me impossible to regard them as forming more than a Family of the Cynodontia.

Within the last eight years I have been so fortunate as to come across a considerable number of new Cynodonts, mostly collected by Mr. A. Brown, and also to add a good many facts to our knowledge of the anatomical structure. Probably the most important of the recent finds has been the discovery by myself of the nearly perfect skull which I have called *Bauria cynops*.

Of all extinct reptilian groups there is probably no one of greater interest than the Cynodontia. Many years ago Owen recognised the remarkable mammalian characters in the Permian and Triassic South African reptiles, and though the Cynodonts were so little known, he ventured to suggest that certain of the Anomodonts were fairly closely allied, and perhaps ancestral, to the Monotremes. Cope held much the same view. When the very much more mammal-like Cynodonts were described by Seeley, many recognised in this higher group the looked for Sauro-Mammalia. Osborn has been the chief advocate of this opinion. Seeley himself, though at first inclining to it, afterwards came to the conclusion that the Mammals were in no way nearly related to the Cynodonts, but sprang from some unknown ancestor that lived in Devonian or Silurian times.

If the Cynodonts are not nearly related to Mammals, the group is still of great interest as showing a marvellous parallelism with the Mammals in skull, teeth, girdles, limbs, and digits; but if, as all recent work seems to indicate still more clearly, the mammalian ancestor was probably a Cynodont, the group becomes vested with an interest altogether unique, and everything bearing on it becomes worthy of the most careful study. I have fortunately been able to examine every known skull, and in the present paper I give the results of my researches. As the paper is morphological rather than systematic, I propose to give a detailed account of the skulls of only the principal Cynodont types, and to consider more fully those points which seem to have a special bearing on the question of mammalian descent.

Bauria.

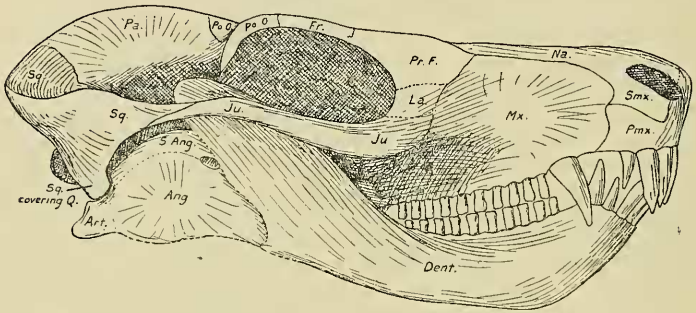
(Pl. XLVI. figs. 6, 7, 8, and text-figs. 168, 169.)

Though *Bauria cynops* occurs in the same horizon as *Cynognathus*, it is the most primitive Cynodont at present known, and may be regarded as the type of a distinct family which may be called the Bauridæ.

As I have just recently, at considerable length, described the only known skull of *Bauria cynops*, it will be unnecessary here to do more than supplement that description in a few details and to consider its relationships to the other known Cynodonts, the Therocephalians, and the Mammals.

Further development and examination of the skull has revealed one or two points not previously noted. Under the nostril and forming not only its floor but covering a considerable part of the premaxillary is a large septomaxillary bone. The lachrymal and prefrontal bones cannot in the specimen be clearly separated from one another, but it is quite manifest that the lachrymal is small and the prefrontal only moderate-sized. The nasal extends well back and forms a broad suture with the frontal. The frontals form the greater part of the interorbital region and most of the supraorbital ridge. There are no postfrontals, and the postorbitals are remarkable in forming only a postorbital process and in not meeting the jugal to form a postorbital arch. The jugal is slender and passes back nearly to the articular region. The portion of the squamosal that supports the quadrate is well developed, but the zygomatic portion is slender.

Text-fig. 168.*



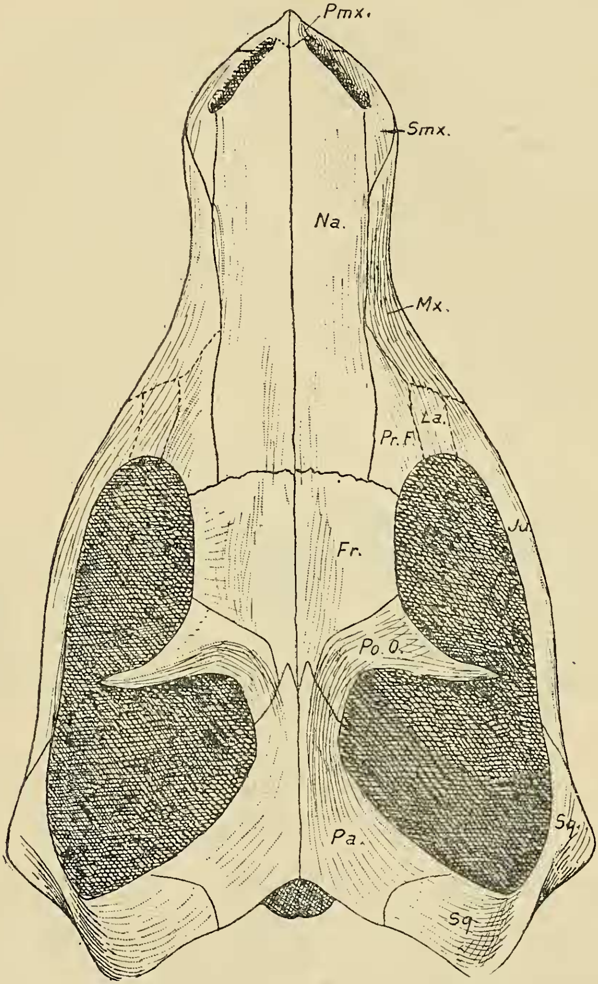
Side view of the type and only known specimen of *Bauria cynops*. Since the specimen was first figured it has been considerably further developed at the British Museum and by myself. The jaws are represented as closed. The molar teeth must meet one another as shown in the figure. When first described the teeth were regarded as round, but further development shows that they are about twice as broad in one diameter as in the other. Though the incisors are mostly broken the impressions of the greater part of each is preserved, and the lower must have met the upper as shown in the figure. The jugal arch is represented in its central part only by the impression, but there is no doubt it must have been practically as restored. It certainly did not meet the postorbital, which is perfectly preserved on both sides. All the sutures shown in unbroken line can be clearly made out.

The palate is as in typical Cynodonts, the secondary palate being as well developed. The vomer, palatines, and pterygoid, so far as can be seen, all are of the ordinary Cynodont type. The lower part of the alisphenoid appears to be of the same type as in higher Cynodonts, articulating with the basisphenoid and passing out to the quadrate. It is just possible, however, that this outward extension may be, as in the Therocephalians, entirely formed by the pterygoid. The basisphenoid is unlike that of either the Anomodonts, Therocephalians, or higher Cynodonts. It is short, with a broad articulation for the basioccipital behind, and a narrow articulation in front for the alisphenoid and probably the vomer. From its under surface there passes down

* For explanation of the lettering in the text-figures see p. 925.

a narrow deep median ridge, which is nearly as deep as the bone is long. The basioccipital resembles considerably that of the Anomodonts in having a pair of short postero-lateral processes

Text-fig. 169.



Upper view of the skull of *Bauria cynops*.

which meet the basisphenoid. The condyle is unique (Pl. XLVI. fig. 8). It is a single condyle, only partly divided into two by a deep median groove. It is thus in type intermediate between the condyle of the Therocephalian and that of the higher Cynodont.

The large foramen for nerves ix., x., xi., and xii. lies by the side of the basioccipital and in front of a bone which is probably part of the opisthotic. Nerve xii. enters the foramen exactly as it does in the higher Cynodonts. On the inside of the skull it has two small distinct canals, which pass forwards and both unite with the large foramen.

The bone which is supposed to be the stapes is shown in fig. 8 (Pl. XLVI). It is apparently a little displaced forwards.

The lower jaw has a fairly large surangular and angular, the dentary being considerably in front of the articular region.

Taking all the characters into consideration, *Bauria* becomes one of the most interesting intermediate types ever discovered. Though an undoubted Cynodont, it retains many of the Therocephalian characters. On the other hand, though on the whole it is less mammal-like than the higher Cynodonts, it has some mammalian characters which the others have lost.

The following are Therocephalian characters usually lost in Cynodonts but retained in *Bauria*:—

1. Large septomaxillaries forming part of the facial surface.
2. Moderate prefrontals.
3. Large frontals forming most of the interorbital region.
4. Feeble zygomatic arch.
5. The two occipital condyles so imperfectly separated as to represent practically a single condyle.
6. Large size of angular and surangular.
7. Shape of the articular.
8. Simple condition of the molar teeth.

In the following characters *Bauria* is nearer to the mammalian ancestor than are the higher Cynodonts:—

1. Large size of septomaxillaries and development on face. A somewhat similar condition is found in primitive Multituberculata (e. g. *Tritylodon*), also in Monotremata, as shown by Gaupp in *Echidna* embryo.
2. Large frontals.
3. Complete loss of parietal foramen.
4. Absence of postorbital arch.
5. Simple condition of molar teeth.

Nythosaurus.

(Text-fig. 170.)

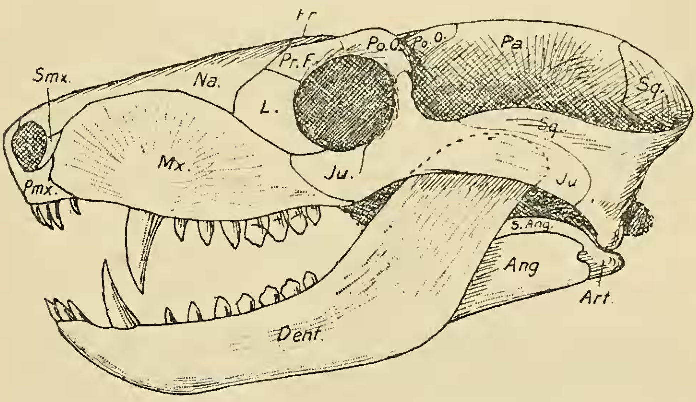
The type of *Galesaurus planiceps* is a somewhat crushed skull with the bones in an unsatisfactory condition for showing sutures. No second specimen of *Galesaurus* has ever been discovered. In 1876 Owen described an imperfect skull as *Nythosaurus larvatus*. In 1887 he described another skull in fairly good preservation which he believed to be another specimen of *Galesaurus*. Seeley in 1894 showed that this supposed second specimen of

Galesaurus differed greatly from the type, and gave it the name of *Thrinaxodon liorhinus.*

There is, in my opinion, not the least doubt that Seeley was right in regarding the 1887 skull as belonging to a very different animal from the 1859 one. In fact it seems strange that any one should ever have thought them the same. *Galesaurus* has a dental formula apparently of i. $\frac{5}{3}$, c. $\frac{1}{1}$, m. $\frac{12}{12}$; the 1887 specimen has a formula of i. $\frac{4}{3}$, c. $\frac{1}{1}$, m. $\frac{7}{7}$. In the 1859 specimen 10 molars occupy 20 mm.; in the 1887 specimen 7 molars occupy 20 mm. But while the two supposed *Galesaurus* specimens represent different genera, two other imperfect specimens in the British Museum show that the 1887 specimen is the same animal as was described in 1876 as *Nythosaurus larvatus.* Hence the well-known skull which is figured in various text-books as *Galesaurus* must in future be called *Nythosaurus.*

Nythosaurus is a much higher type than *Bauria*: but though it comes fairly close to the higher Cynodonts such as *Cynognathus*, it should, I think, be taken as the representative of a distinct family, the *Galesauridæ.* From the various specimens in the British Museum it is possible to make an almost complete restoration of the skull.

Text-fig. 170.



Side view of the skull of *Nythosaurus larvatus.* The drawing is mainly that of the best preserved specimen in the British Museum, compared with the other specimens and slightly restored from them. The teeth are represented in the mature condition.

The septomaxillary though smaller than in *Bauria* still appears on the face. The nasal is large and very broad at its upper end. The lachrymal is large, and though the prefrontal is only of moderate size, it joins with the postorbital and completely shuts out the frontal from the orbit. The postorbital forms with the jugal a rather feeble postorbital arch. The zygomatic arch is formed by the jugal and the squamosal. The jugal extends nearly back to the articular region, and the squamosal nearly forward to the base of the postorbital arch. The squamosal is not unlike that of *Bauria*, but the zygomatic portion is much better developed; so that as regards the squamosal *Nythosaurus* is intermediate between *Bauria* and *Cynognathus*. The quadrate is of the same type as in the better known *Cynognathus*.

The palate, so far as known, agrees fairly well with the *Cynognathus* type, and the occipital condyle is double.

The lower jaw has a large dentary, but there is no trace even of a condylar process. The angular and surangular are fairly large and still resemble considerably the Therocephalian type. The articular also resembles that of the earlier rather than that of the later types.

Nythosaurus is perhaps the most mammal-like of the known Cynodonts. The zygomatic arch is exceedingly like that of most primitive mammals, and if the prefrontal and postorbital bones were lost and the internasal process of the premaxilla aborted there would be nothing left in the side view of the skull to distinguish it from that of a mammal. The lower jaw with its fairly large angular and surangular is still much less like the mammalian condition than what we see in the higher Cynodonts, and the articular is of the same primitive type seen in *Bauria*.

The dentition though very primitive is considerably more highly evolved than in *Bauria*. The formula, i. $\frac{4}{3}$, c. $\frac{1}{1}$, m. $\frac{7}{7}$, comes very near to that of the typical mammal, and that of *Galesaurus*, i. $\frac{5}{3}$, c. $\frac{1}{1}$, m. $\frac{12}{12}$, is near that of the ancestral mammal. The difference in the teeth in some of the specimens of *Nythosaurus* is apparently due to the fact that in some the teeth belong to the first set and in others to the second.

Cynognathus.

(Pl. XLVI. figs. 1 & 2, and text-figs. 171, 172.)

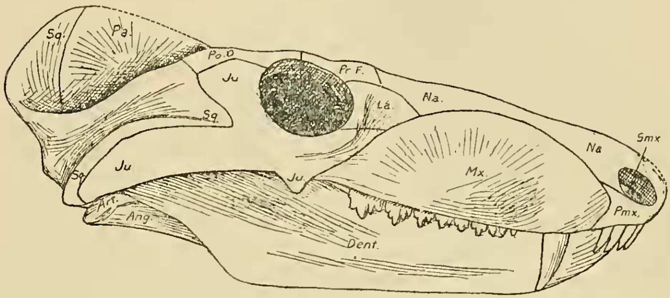
The genus *Cynognathus* is known by the very fine skull of *C. crateronotus* in the British Museum, the type skull of *C. platyceps* in the Albany Museum, a fairly good skull of *C. berryi* in the S. African Museum, and three or four less satisfactory specimens.

Seeley has given a fairly full account of the skull of *Cynognathus crateronotus*, but unfortunately a number of his figures are so indifferently reproduced that they convey no more to the student than does the plaster cast. And further, while most of his determinations are correct, he unfortunately suggests so many alternative possibilities that the morphologist is left comparatively helpless.

The figure given by Seeley of the side view of the skull of *C. crateronotus* gives an excellent idea of the general form of the skull and of the structure of the temporal region, except that the supposed perforation in the zygomatic arch is, in my opinion, not a natural feature and has been produced post mortem. The side view which I give of the skull of *C. platyceps* is fairly similar, except that the skull is here much broader and flatter, and in this species, at least, there is no trace of an opening in the zygoma.

The snout of *Cynognathus* differs from that of *Bauria* and *Nythosaurus* chiefly in the fact that the septomaxillary does not appear on the face, though it can be readily seen within the nostril.

Text-fig. 171.



Side view of the skull of *Cynognathus platyceps*. With the exception of the front of the snout the drawing is made from the very fine type skull in the Albany Museum. The front of the snout is from the specimen described by Seeley as ? *Cynognathus leptorhinus*. As I showed some years ago, this is unquestionably the snout of a nearly full-grown specimen of *Cynognathus platyceps*.

The premaxilla is relatively rather larger than in *Nythosaurus*, while the maxilla is about equally well developed in the two genera. The canine is, however, much further forward in *Cynognathus* than in the smaller genus.

The nasal bone is fairly similar in the two genera, being broad both in front and behind and narrow in the middle.

The lachrymal extends further forward than in *Nythosaurus*, the portion showing on the face being nearly as large as the orbit.

The prefrontal is a long narrow bone which forms the greater part of the upper margin of the orbit, and by meeting with the postorbital completely shuts out the frontal from the orbital margin.

The frontals are each about four times as long as broad. In front they meet the nasals. Laterally they are in contact with the prefrontals and postorbitals. Posteriorly they taper away to narrow points, which meet the anterior ends of the parietals.

The postorbital is a large triangular bone. In front it meets the prefrontal and forms part of the orbital margin. Externally it gives a large articulation to the jugal and a small articulation to the squamosal. Internally it overlaps the parietal for only a very short distance.

The jugal is relatively considerably larger than in *Nythosaurus*. Anteriorly it meets the maxilla and lachrymal, but extends further forward than in either *Nythosaurus* or *Bauria*. Immediately below the orbit there is a small but very distinct tubercle. The ascending process of the jugal is unusually broad and forms a large articulation with the postorbital, the two together forming a very strong postorbital arch. The posterior portion of the jugal extends to the articular region.

The parietal is a narrow bone which forms a low median crest. There is a small pineal foramen.

The squamosal is the largest bone in the skull, with the exception of the dentary. The inner and posterior portion forms nearly the whole of the back wall of the temporal fossa, and has a large articulation with the parietal. This back portion of the squamosal is very thin and is closely united with the flat upper expansion of the opisthotic. The squamosal forms the outer wall of the lateral occipital foramen. Inferiorly it meets the exoccipital and on passing outwards supports the small quadrate. The zygomatic portion is much larger than in *Nythosaurus*, articulating with the whole of the upper side of the posterior limb of the jugal and meeting the postorbital. There is a deep groove along the middle of the back part of the zygomatic portion, which curves downwards and inwards, and, most probably, the posterior part was for the support of the external auditory canal.

The occiput is best known from the specimen of *Cynognathus berryi* in the S. African Museum, which though imperfect shows the sutures very distinctly. The large occiput figured by Seeley* (p. 130) and doubtfully referred by him to *C. berryi*, is, in my opinion, considerably too large. It also differs from the known occiput of *C. berryi* in the shape of the foramen magnum, the slope of the exoccipitals, and the moulding of the interparietal region. It is pretty clearly not the occiput of *C. crateronotus*, while it is much too large to be that of *C. platyceps*. As it thus seems to belong to a new species, it may appropriately be named *Cynognathus seeleyi*.

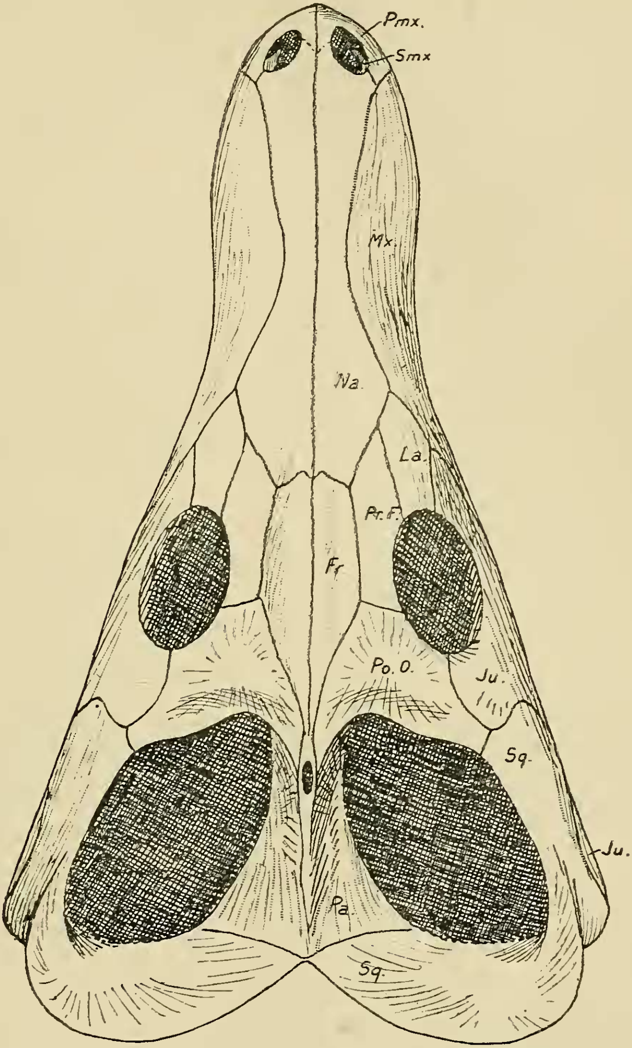
The occiput proper (Pl. XLVI. fig. 2) is made up of seven bones, or, if we include the squamosals, nine. About a quarter of the occiput proper is formed by a median bone, which is apparently the interparietal. I have not seen any specimen which enables me clearly to differentiate this bone from the parietal in front, but, judging by analogy and by the direction of the fibres of the bone, the probability seems much in favour of its being a distinct interparietal.

On either side of the interparietal is articulated a large bone, which is apparently the opisthotic. Its occipital portion is comparatively thin and to a considerable extent covered in front by

* Phil. Trans. Vol. clxxxvi. B. (1895).

the squamosal and parietal. Inferiorly it articulates with the exoccipital and to a large extent with the supraoccipital. It

Text-fig. 172.



Upper view of the skull of *Cynognathus platyceps*.
From the same specimen as text-fig. 171.

forms the upper and inner wall of the lateral occipital foramen, and passes well forward below the edge of the parietal and appears to articulate with the large prootic.

The supraoccipital is completely anchylosed to the exoccipitals, but its probable limits are indicated in the figure given. Immediately above the foramen magnum is a small rounded bony knob.

The exoccipitals form the greater part of the occipital condyles, which are remarkably mammal-like. Above each condyle is a narrow fissure or groove leading into the foramen magnum, but it seems too small to have been for the transmission of either an artery or a vein, and most probably it was not for a nerve. Possibly it is merely owing to the elevation of a portion of the bone for the attachment of a ligament. The exoccipital passes out a considerable distance under the lateral foramen and articulates with the squamosal.

The quadrate is well shown in Seeley's figure 8. It is a relatively small bone, which is firmly fixed on to the squamosal by the main part being in front and two long processes being behind its lower projection. Referring to the posterior delicate processes Seeley says: "I am unable to affirm that they represent auditory ossicles." They are unquestionably parts of the quadrate and have nothing to do with the auditory function. The quadrate forms the greater part of the articular surface for the lower jaw, but not the whole of it, part of the squamosal also forming a portion of the articulation. This is particularly interesting in view of the fact that in the Monotremes the lower jaw hinges directly on the squamosal bone.

The palate of *Cynognathus* is nearly wholly known, the only points concerning which we are still ignorant being the relations of the bones round the anterior palatine foramina, the nature of the middle part of the basicranium, and the relations of the palatine and pterygoid to the jugal.

There is a large secondary palate formed by the maxillæ and palatines exactly as in Mammals. In a recent paper Seeley describes what he believes to be teeth on the palate of *Cynognathus*. I have, however, had an opportunity of examining Seeley's specimen and believe the supposed teeth to be merely irregularities of the bony surface, possibly pathological. Certainly in the other specimens I have examined there is no trace of anything like teeth. The hard palate ends in the middle line opposite the front of the third last molar.

The pterygoids are large and have well-developed pterygoid processes, which lie close along the inside of the jaws as in reptiles generally. There is no transpalatine or ectopterygoid bone. Instead of, as in most reptiles, the pterygoid having a posterior process which extends to the quadrate, it here ends near the middle of the inner wall of the temporal fossa, the posterior continuation which looks like pterygoid being really part of the alisphenoid bone.

The vomer is a large median bone which posteriorly lies between the two pterygoids. In front it forms a vertical plate which supports the secondary palate exactly as in Mammals and extends to near the front of the snout.

The alisphenoid bone is one of the most interesting bones in the skull. It is a large flat bone which extends from the pterygoid below to the parietal above. It is well seen in the type skull of *Cynognathus crateronotus*, but even better in the Capetown specimen of *C. berryi* (Pl. XLVI. fig. 1). The upper portion of the bone is irregularly quadrilateral. The upper side articulates with the parietal, and the posterior with what I believe to be the prootic. Between the alisphenoid and the prootic are two large oval foramina. At the posterior and lower corner the alisphenoid is continued as a slender bone to the quadrate. At its anterior and lower corner it meets the pterygoids and clasps the basisphenoid. There appears to be an opening into the brain-cavity between the base of the alisphenoid and the basisphenoid.

The basisphenoid is clasped by the alisphenoids and meets the basioccipital posteriorly.

The basioccipital is a small bone lying behind the basisphenoid. It forms the middle part of the occipital condylar region. On each side there is a large round foramen which is pretty certainly the foramen for the exit of nerves ix., x., xi., and xii.

Between the outer part of the basioccipital and the quadrate there stretches a rounded pillow-like bone concerning which there may be some difference of opinion. I believe it to be the stapes, for reasons which will be stated later.

The lower jaw is remarkable for the great size of the dentary, which posteriorly nearly reaches the articulation. Elsewhere I have dealt at some length with the structure of the jaw. The splenial is long and slender. The surangular and angular are also feeble splint-like bones. The articular is fairly well developed but short. I cannot satisfy myself that there is a distinct coronoid bone as is stated by Seeley.

The only points in which the *Cynognathus* skull is nearer to the mammal than that of *Bauria* and *Nythosaurus* are: (*a*) the closer approach of the jugal to the articulation, (*b*) the greater development of the dentary, (*c*) the greater reduction of the angular and surangular, and (*d*) the more mammal-like occipital condyle. On the whole it is not so near the mammalian ancestor as either *Bauria* or *Nythosaurus*.

The dental formula appears to be i. $\frac{4}{3}$, c. $\frac{1}{1}$, m. $\frac{9}{9}$.

Trirachodon.

(Text-figs. 173 & 174.)

Trirachodon is best known by the type skull which is in the Albany Museum. Though the skull is immature and much crushed it is practically perfect. Two or three other known skulls though imperfect show the uncrushed condition of the greater part of the adult skull.

The premaxilla is smaller than in *Cynognathus*, not meeting the nasal behind the nostril, at least not on the face.

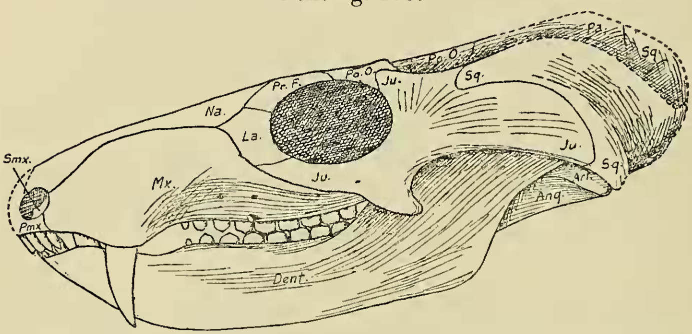
The septomaxillary is entirely in the nostril, forming no part of the face.

The maxilla is long and extends far back below the orbit. The snout is fairly broad at the root of the canine and along the upper part of the maxilla, but is much narrowed in the molar region. There are two foramina for the maxillary branch of nerve v.

The nasal is moderately broad in front, narrow in the middle, and very broad behind.

The lachrymal is small, but forms most of the anterior wall of the orbit.

Text-fig. 173.



Side view of the skull of *Trirachodon kannemeyeri*. The drawing is chiefly founded on the crushed and immature skull which forms the type. Two mature and uncrushed but imperfect skulls in the Albany Museum and a good snout in my own collection have made it possible to correct the crushing of the type and completely restore the skull in the adult condition.

The prefrontal is about twice as long as broad, and forms most of the upper margin of the orbit; it unites, as in *Cynognathus*, with the postorbital, completely shutting out the frontal from the orbital margin.

The frontal is fairly like that of *Cynognathus*, but it does not extend so far forward. Posteriorly, as in the former genus, it tapers away between the postorbitals.

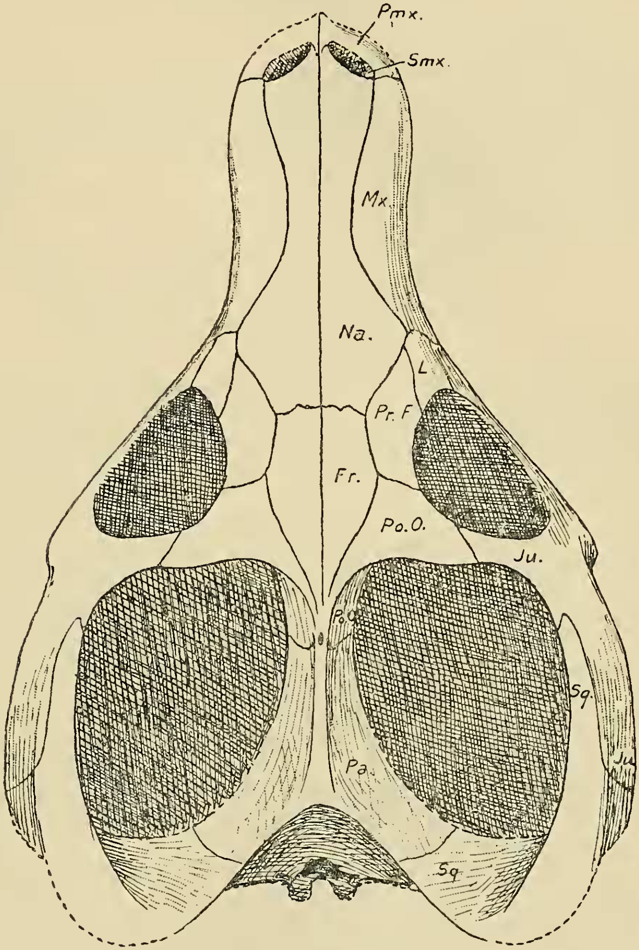
The postorbital is more like that of *Nythosaurus*. It forms the upper third of the postorbital arch, uniting with the jugal. It extends backwards on the side of the parietal a little beyond the pineal foramen.

The parietal is like that of *Cynognathus*, but the pineal foramen is much smaller.

The jugal is, on the whole, like that of *Cynognathus*. It has, however, the inferior process much better developed. It forms the lower and posterior half of the orbital margin.

The squamosal differs from that of *Cynognathus* in not meeting the postorbital, but ending in front above the jugal, very much as in *Nythosaurus*. As the back of the skull is relatively narrower than in *Cynognathus*, the posterior part of the squamosal differs considerably in contour.

Text-fig. 174.



Upper view of the skull of *Trirachodon kannemeyeri*.
From the same specimens as fig. 173.

The quadrate, so far as can be seen, is small but not unlike the better known types.

The stapes is a very slender straight bone about the thickness of a pin, and having similar relations to the stapes in *Cynognathus*.

The occiput is not well known, but is apparently very similar to that of *Cynognathus*.

The lower jaw has a very large coronoid process and a condylar process which nearly reaches the articulation. The articular, angular, and surangular are on the whole very similar to those of *Cynognathus*.

One of the most striking points of difference from *Nythosaurus* and *Cynognathus* is in the structure of the molar teeth, which have flattened tops, and the lower molars instead of passing inside of them, as in these other genera, meet them much in the same way as do the molars in Mammals.

The dental formula is the same as in *Cynognathus*, viz.: i. $\frac{4}{3}$, c. $\frac{1}{1}$, m. $\frac{9}{9}$.

Diademodon and *Gomphognathus*.

(Pl. XLVI. fig. 9, & text-figs. 175–178.)

Diademodon resembles *Gomphognathus* so closely, differing only in size and in the number of molars, that there is some reason for suspecting that *Diademodon* may be an immature *Gomphognathus*. If this turns out to be the case, the genus must take the earlier name *Diademodon*. The following description of a skull is based on a beautifully preserved skull in the British Museum, which may be called *Gomphognathus minor*, but which unfortunately has lost the snout, on a fairly good skull of *D. mastacus* in the South African Museum, on two other good skulls of *Gomphognathus* in the British Museum, and on the type skull of *Gomphognathus kannemeyeri* in the Albany Museum. As the result of the examination of this very fine material, the *Gomphognathus* skull is better known even than that of *Cynognathus*, and almost as well as that of the living *Ornithorhynchus*.

The premaxilla is fairly large, but, as in all other Cynodonts, considerably overlapped by the front of the maxilla. It has a strong internasal process, and forms the anterior and most of the lower border of the nostril. It has a very considerable palatal development, the two bones meeting in the middle line behind the anterior palatine foramen.

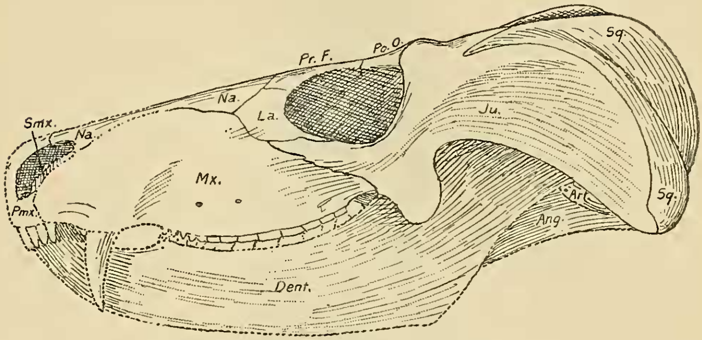
The septomaxillary is well developed, lying along the greater part of the outer wall of the nostril. Most of it is within the nostril, but a small part of the upper end appears on the face.

The maxilla is not unlike that of *Trirachodon*. The maxillary branch of nerve v. has two foramina. On the upper part of the maxilla close to the nasal is a small oval depression, presumably for the lodgment of a gland.

The nasal is narrow in front but broad behind. The nostrils look more upwards than in any of the previously described Cynodonts, and the nasal passes forward between them to a narrow process.

The lachrymal is of fair size. In *Gomphognathus minor* it forms the front of the orbit and much of the inner wall. In *Gomphognathus polyphagus* it is considerably larger, extending to part of the upper margin.

Text-fig. 175.



Side view of the skull of *Gomphognathus minor*. With the exception of the front half of the snout and the lower jaw, the drawing is from the beautifully preserved type in the British Museum. The front of the snout is restored from a specimen of *Gomphognathus kannemeyeri* in the British Museum, and the lower jaw is from the lower jaw of the type of *G. kannemeyeri* in the Albany Museum. Both these latter are slightly modified to fit the skull of *Gomphognathus minor*.

The prefrontal forms most of the upper margin of the orbit. In *Gomphognathus polyphagus* it is considerably smaller than in *G. minor*, owing to its being encroached on by the larger nasal and lachrymal. By uniting with the postorbital it completely shuts out the frontal from the orbital margin.

The frontal is relatively small, the two together forming only about one-third of the interorbital space. As in all the other Cynodonts except *Bauria* and *Sesamodon*, the frontals posteriorly taper away to a point between the postorbitals.

The postorbital is a fairly large bone with an external limb which meets the jugal, forming the postorbital arch, and a posterior process which lies along the parietal. In *G. polyphagus* the postorbital bar is relatively slenderer than in *G. minor*.

The jugal is very large. It is essentially similar to that of *Trirachodon*. The inferior process is much larger and the posterior extension much deeper. It passes backwards some distance behind the plane of the quadrate.

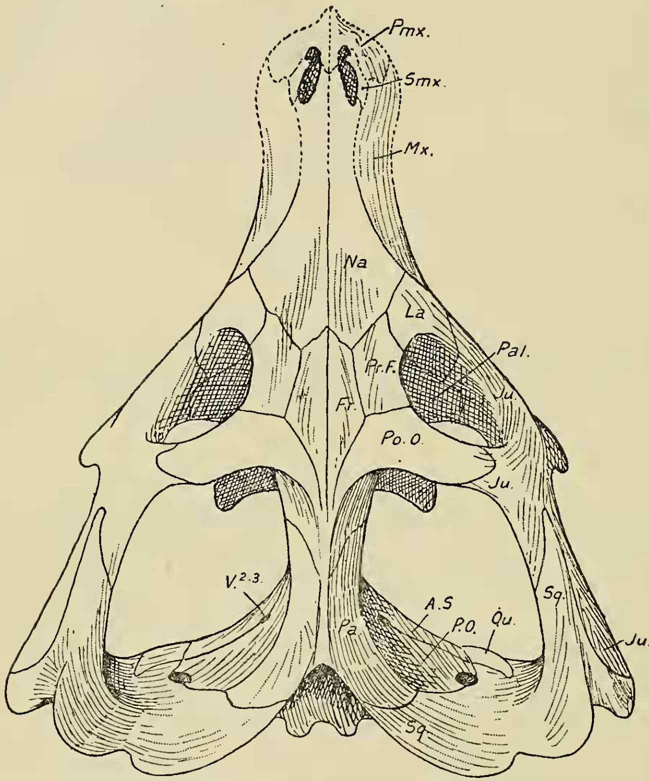
The parietal is small and there is a small pineal foramen.

The squamosal is extremely large. The inner portion articulates with the parietal. The outer and anterior portion lies above the jugal, forming with it a powerful zygomatic arch. Inferiorly the squamosal supports the small quadrate. The peculiar shape of the bone can best be understood from the figures.

The occiput is very similar to that of *Cynognathus*, but the limits of the various elements are less satisfactorily known. The condyle is double, but is relatively smaller and less mammal-like than in *Cynognathus*.

The palate is beautifully shown in three of the British Museum specimens.

Text-fig. 176.

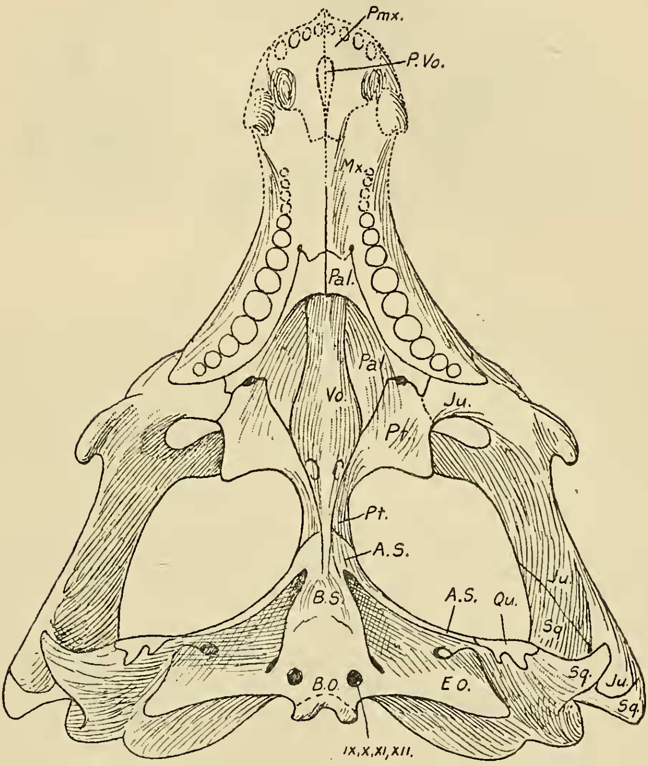


Upper view of skull of *Gomphognathus minor*.
The snout restored from *Gomphognathus kannemeyeri*.

In the anterior palatine opening there is a pair of narrow bones showing what I suggested a good many years ago were probably prevomers. Only one specimen is known in which they are shown. They are evidently not parts of the premaxillæ, and as they are in position exactly corresponding to the prevomers of *Ornithorhynchus*, I am still of opinion that they correspond to the paired vomers of most reptiles and the prevomers of *Platypus* and of *Miniopterus*.

The secondary palate is almost typically mammalian, the maxillæ and the palatines having the same relations as in the mammal. The palatine besides forming part of the secondary palate curves round inside of the maxilla, forming the outer wall and part of the roof of the posterior nares. There is a posterior palatine foramen situated exactly as in Mammals.

Text-fig. 177.

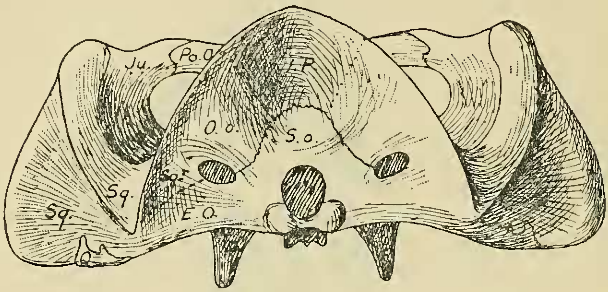


Under view of skull of *Gomphognathus minor*.
The snout restored from *Gomphognathus kannemeyeri*.

The vomer is large and, as in typical Mammals, it forms the median support of the basicranial axis from the sphenoidal region to near the front of the nose. It forms about one-third of the roof of the pharynx, and two small tubercles on its posterior part are probably for the attachment of pharyngeal muscles. In the region of the secondary palate the vomer forms for a considerable distance a median support.

The pterygoid is of moderate size, but much smaller than in any other reptilian group. In front it meets the jugal and the palatine and lies along the outer side of the vomer. It forms a large descending pterygoid process. Posteriorly it lies against the vomer and terminates by meeting the alisphenoid as in *Cynognathus*.

Text-fig. 178.



Posterior view of skull of *Gomphognathus minor*.

The basioccipital, basisphenoid, and exoccipital are all apparently very similar to those bones in *Cynognathus*. There is a large foramen for the exit of nerves ix., x., xi., and xii. Outside of this foramen, but further from the base, is another foramen which I believe to be the fenestra ovalis, but this is less certain than the nature of the larger foramen, about which there is no doubt.

The alisphenoid in all its relations is very similar to that in *Cynognathus*. At its lower end near where it meets the pterygoid is an opening which leads into the brain-cavity, and most probably it was by this opening that the internal carotid artery entered the cranium.

The quadrate is relatively rather smaller than in *Cynognathus*, but is fixed into the squamosal bone in a very similar fashion. It clasps the lower margin of the bone, and posteriorly it has two processes which fit into grooves. In the type specimen of *Gomphognathus kannemeyeri*, where the articulars do not fit on to the quadrates, I thought the quadrates had been displaced, but I am rather inclined to think it is the articulars, as the London specimens show that the quadrate is not likely to be readily disarticulated.

In the median section of the skull (Pl. XLVI. fig. 9) a number of most interesting features are revealed. In the posterior cranial region there are seen the foramina for the exit of a number of the cranial nerves. Close to the occipital condyle are two small foramina for nerve xii. These after passing a short distance through the bone open into the large foramen lacerum posticum. This large foramen is also situated well back and doubtless transmitted also nerves ix., x., and xi. In front of this foramen jugulare is the prootic bone, which appears to have two foramina in it. The posterior I believe to be for nerve viii., and the anterior for vii. Between the prootic and the large alisphenoid is seen the opening for probably both the 2nd and 3rd branches of nerve v. Immediately below this foramen, the prootic sends a sharp bony process upwards, inwards, and forwards. Probably it lay on the inner side of the Gasserian ganglion.

The basisphenoid is a large bone, along the front of which lies the back part of the vomer. There is no orbito-sphenoid and no presphenoid bone.

The vomer passes from the basisphenoid to about the middle of the hard palate. Along its dorsal surface ran the cartilaginous cranial axis, against which the grooved upper surface of the vomer fits. At the front of the vomer the median cartilage is ossified, and the bone is apparently the homologue of the mammalian mesethmoid. In the figure given of the median section the prevomer (*P.vo.*) and the septomaxillary (*Smx.*) are largely hypothetical.

Sesamodon and *Melinodon.*

(Pl. XLVI. figs. 3, 4, & 5, and text-figs. 179, 180.)

These two allied genera, which are both unfortunately very imperfectly known, stand at present by themselves some distance apart from the other Cynodonts. Each genus is known only by a single specimen, which in the case of *Sesamodon browni* is only fair, and in the case of *Melinodon simus* very poor. Still the interest attaching to the specimens is so very great that it is necessary to figure them as fully as possible.

Though the only known skull of *Sesamodon browni* is very badly weathered and considerably crushed, it is fortunately possible to restore the external appearance with much certainty. In fact the only points in the external anatomy that remain in doubt are the articular region, the middle of the occiput, and parts of the jugal, frontal, parietal, and squamosal bones.

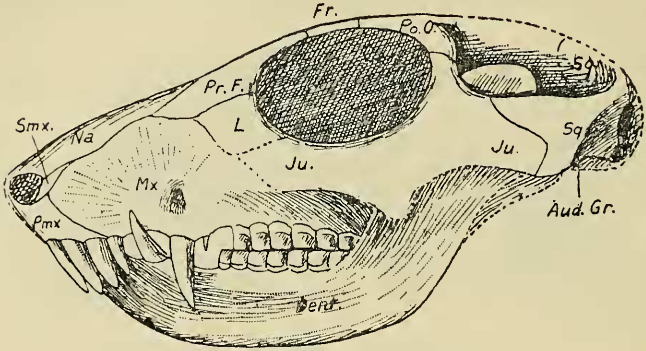
The premaxilla is not very satisfactorily preserved, but presents no unusual features.

The septomaxillary is apparently fairly similar to that of *Nythosaurus*, appearing on the face to a considerable extent.

The maxilla is large and resembles to some extent that of *Trirachodon*, while in other respects it is nearer to *Nythosaurus*. The canine is relatively smaller than in either *Trirachodon* or *Nythosaurus*, but is situated, as in *Nythosaurus*, far back from the front of the bone. The molars, with the exception of the 1st which is small, form a uniform series, and the maxillary bones are much approximated in the molar region, as in *Trirachodon*.

The nasal resembles on the whole that of *Bauria*. The nostril is directed mainly forward and the nasal to some extent overhangs it. The bone is moderately broad throughout its whole length, but is chiefly remarkable in being narrower behind than in front. In all other Cynodonts except *Bauria* the nasal is, as in Marsupials, much broader posteriorly.

Text-fig. 179.



Side view of skull of *Sesamodon browni*. Somewhat restored from the only known specimen, which forms the type. The whole of the preorbital portion of the skull except the front of the premaxilla is preserved in the specimen, though the bone in parts is weathered off, leaving only the impression. Though the teeth are imperfect, remains or impressions of all are present, so that the full dentition can be restored with much certainty, the only doubt being the exact length of the incisors and canines. The orbit and the temporal fossa are satisfactorily preserved, and the squamosal is fairly well preserved on the right side of the skull. The lower border of the jugal is unknown. Both mandibles are in position but much weathered. The horizontal ramus is fully known, but much of the ascending ramus is lost. As, however, the top of the coronoid process is preserved in position, the greater part of the dentary can be restored with certainty. The condylar process is badly preserved. A considerable part of what is believed to be the angular and probably part of the articular are preserved. As the position of the glenoid cavity is known, the general shape of the back of the jaw can be restored with some probability.

The lachrymal is small and completely separated from the nasal by the prefrontal. In this, *Sesamodon* again agrees with *Bauria* and differs from all other known Cynodonts.

The prefrontal is much larger than the lachrymal and meets the frontal, nasal, maxilla, and lachrymal as in *Bauria*.

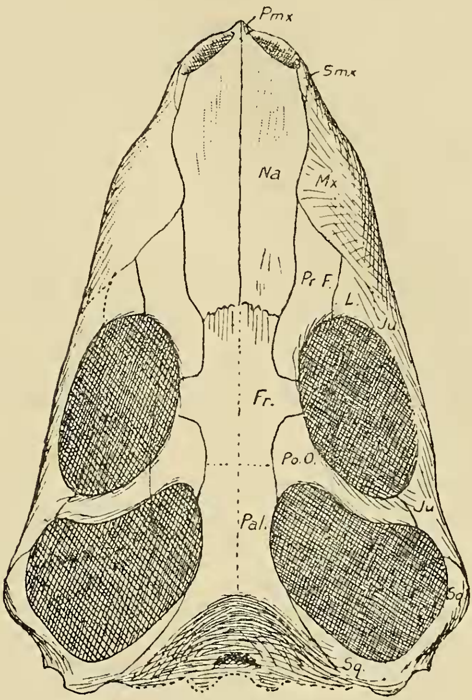
The frontal is almost completely lost from the specimen, but just sufficient of the impression of the bone is left to show that it reached the orbit as in *Bauria*. In this also, *Sesamodon* differs from almost all other known Cynodonts.

The postorbital is fairly large but slender. It forms with a small part of the jugal a complete postorbital arch. It only extends backwards on the parietal a very short distance.

The parietal is completely lost except just sufficient to show the width of the bone.

The jugal is not well preserved except in the upper part. It forms the whole of the lower orbital margin and part of the postorbital arch. In the drawing given the lower margin is entirely hypothetical. The posterior or zygomatic portion of the bone is very short.

Text-fig. 180.



Upper view of skull of *Sesamodon browni*, restored from the type. From the specimen the whole of the frontals, parietals, and most of the occiput have weathered away, so that these parts are unknown. As, however, the prefrontals, postorbitals, and the margins of the orbits and temporal fossæ are preserved, the only points that are left in doubt are the position of the fronto-parietal suture, whether there is a parietal foramen, and the nature of the condyles.

The squamosal is sufficiently well preserved to show its main features, and it is seen to be unlike that of any other Cynodont. As in *Bauria* it is much smaller than in the higher types. It articulates, as in other forms, with the parietal, but on passing outwards it has not, as in *Bauria*, a posterior ridge. The zygomatic portion is much shorter than in *Bauria* or any other known type, but it is relatively fairly deep.

What appears to be the quadrate is a small flattened bone which I have shown in the figure, but the parts are crushed and somewhat displaced, and it is impossible to speak with certainty of the condition.

The occiput is badly preserved, but is remarkable for the great lateral extension of the exoccipital, which passes out behind and below the squamosal. Owing to some degree of crushing it is difficult to be quite sure of the relations of the external end of the exoccipital, but it certainly extends much further out than in any other known Cynodont.

The palate, so far as preserved, differs considerably from that of the typical Cynodonts. There is a secondary palate of the ordinary type, but the pterygoid appears to have a larger pterygoid process than usual. Behind the pterygoid process there is a fan-like bony expansion which passes backwards and outwards towards the articular region. It looks as if it might be all pterygoid, but owing to the crushed and weathered condition of the specimen it is impossible to be sure. Possibly, as in the typical Cynodonts, it is part of the alisphenoid.

The structure of the lower jaw cannot be satisfactorily made out. The dentary has a very large coronoid process; in fact the coronoid process is as large as the horizontal ramus. There also is some evidence of a condylar process. The articulation is apparently, mainly at least, formed by a rounded articular supported by possibly an angular and surangular. There is a well-developed splenial bone.

The dental formula is i. $\frac{4}{3}$, c. $\frac{1}{1}$, m. $\frac{7}{7}$.

Melinodon is closely allied to *Sesamodon* and pretty certainly belongs to the same family. The teeth are of the same type, but relatively much smaller. The specimen is so imperfect that it is impossible to make much of the skull. I have figured it as preserved (Pl. XLVI. fig. 3).

Sesamodon resembles *Bauria* and differs from the other Cynodonts in the following characters:—

1. The nostril is directed more forwards than outwards.
2. The nasal is not widened posteriorly.
3. The prefrontal is larger than the lachrymal and prevents the lachrymal from meeting the nasal.
4. The frontal forms part of the orbital margin.
5. The postorbital arch is feeble: incomplete in *Bauria*.
6. The molars show no sign of cusps.

In the following characters *Sesamodon* comes nearer the Mammals than any of the other known Cynodonts:—

1. An articulation for the lower jaw which permits of some degree of antero-posterior movement.
2. The lower canine lies outside the edge of the maxilla when the jaw is closed.

In addition to the mammalian characteristics peculiar to *Sesamodon*, it combines most of those mammalian characters seen in *Bauria* with most of those found in the other higher Cynodonts.

Peculiarities of the Mammalian Skull, apparently derived from a Cynodont Ancestor.

Most of the bones of the mammalian skull have their homologues in the Labyrinthodont skull, but they are also to be found in the skulls of most reptiles. There is, however, no close resemblance between the mammalian and the batrachian bones, and in many cases the differences in cranial structure are so great that the gap between the mammal and any known batrachian must be enormous. When we examine the Cotylosaurian skull, we find that the resemblance to that of the mammal is still remote, but any little resemblance there was in the Labyrinthodont is here increased, while there are many mammal-like characters not seen in the lower type.

The Pelycosaurians of the Lower Permian are so much more mammal-like than any of the lower forms that, notwithstanding their remarkable specialisations, one cannot help feeling, as Cope felt, that here were forms fairly near to the remote mammalian ancestor.

The Therocephalians and Anomodonts of the Middle Permian times are in essentials still more mammal-like. For the first time we get a dentition clearly divided into incisors, canines, and molars; for the first time we get a lower jaw with a dentary which has a large coronoid process. We get a zygomatic arch formed on the mammalian type, and we lose for the first time the quadratojugal. We also get most marked mammalian characters in the postcranial skeleton.

The Therocephalians survived into Upper Permian times, but hitherto they have not been found in Triassic beds. In Upper Triassic times their place was taken by the Cynodonts. Though the gap between the Therocephalians at present known and the Cynodonts is very considerable, the primitive Cynodont *Bauria* is to some extent a connecting link.

Almost all the characters in which the Cynodont skull differs from the Therocephalian are characters which are met with in Mammals. Of these the most noteworthy are:—

1. Formation of a secondary palate.
2. Vomer very large, extending forward as a support to the secondary palate.
3. Great reduction or complete loss of prevomers (*Bauria*).
4. Loss of the postfrontal bone.
5. Great reduction or loss of the pineal foramen.
6. Two occipital condyles.
7. Reduction of the quadrate.
8. A large alisphenoid bone instead of the homologous rod-like "epipterygoid" or columella cranii of the Therocephalians and Anomodonts.
9. Pterygoids not extending back to the quadrates, the posterior extension being replaced by the alisphenoids.
10. Reduction of the angular and surangular, and greater development of the dentary.

The presence of this large number of mammalian characters in the Cynodont skull, and the absence of any in either skull or skeleton that might not have been expected in the mammalian ancestor, make the case very strong for the mammalian ancestor having been a Cynodont. But the evidence becomes even stronger when we find that most of the peculiarities, even minor peculiarities, of the mammalian skull have light thrown on them by the condition of affairs in the Cynodont skull.

Let us consider some of the more remarkable characters of the mammalian skull in the light of our knowledge of the Cynodont.

Premaxillary.

One of the most striking peculiarities of the mammalian skull is that the nostrils are separated only by cartilage, so that if the cartilage be removed the nostrils are united. In most reptiles, in birds and amphibians the nostrils are divided by an upward and backward process of the premaxilla, the internasal process. As it is present in Cotylosaurs, Dromasaurs, Pelycosaurs, Therocephalians, Anomodonts, and even Cynodonts, one might fancy that here was evidence against the Cynodont ancestry. But there is good reason to believe that the early Mammals retained the internasal process and that it was only lost after the Mammals were well established.

In both *Ornithorhynchus* and *Echidna* the young animal has an internasal process developed on the premaxilla almost exactly as in reptiles. The fact that it is retained as a support to the caruncle or egg-tooth in no way invalidates the conclusion that it is the reptilian internasal process that has been retained. For there cannot have been a time when there was a caruncle without a support, and thus the internasal process must be as old as the caruncle. As we may be pretty certain that the mammalian ancestor was oviparous, we may safely conclude that the internasal process is not a neomorph, but the reptilian structure handed on.

In *Tritylodon* there is an imperfect but distinct little internasal process. The only known specimen is too imperfect to enable me to say whether it formed a complete though slender process which joined with the nasals. Even if it did not in the adult, it is rather probable that it did in the very young animal, since *Tritylodon* is so much more primitive than the marsupial that not improbably it was oviparous.

In the skulls of young Diprotodonts (e. g. *Macropus*) a rudiment of the internasal process is usually present. And in the young *Trichosurus* at birth the internasal process, as I recently pointed out, can be traced right round in front of the nose. In the very young marsupial, the nostrils are entirely lateral and wide apart, and the nasal cartilages pass round in front of each, leaving a sulcus in the middle line between the two. The premaxillaries send up short processes along the sulcus, but from the ends of the processes two strands of condensed but unossified cells can be easily traced round to the top of the snout. Were these tracts ossified we would have a condition practically similar to that of the Cynodont.

Septomaxillary.

Kitchen Parker many years ago recognised this as a distinct membrane-bone in the Lizards and Snakes, but it is only recently that much attention has been paid to it, chiefly as the result of the work of one or two palæontologists in Europe and America. The bone is not known in Labyrinthodonts and probably does not occur in the Amphibia (the supposed septomaxillary of *Xenopus* being probably not homologous). We find it, however, in the very earliest true reptiles, and we can trace it on the one hand through numerous members of the Diapsida, and on the other through most of the mammal-like Reptiles on to Mammals.

A septomaxillary has been found in *Pareiasaurus*, *Pariotichus*, and *Procolophon*. In these primitive genera it is mainly within the nostrils, and probably fulfils its main function as a roof to Jacobson's organ.

When we come to the mammal-like Reptiles, we find it in the Pelycosaurs still mainly within the nostril. In the Dinocephalians (*Delphinognathus*, *Tapinocephalus*) it comes partly on to the face. In the Dromasaurians (*Galepus*), it forms a very appreciable portion of the facial wall; and in the Therocephalians (*Scylacosaurus*, *Aloposaurus*), it also appears pretty largely on the face. In the Anomodonts it is absent, probably because they had lost their organ of Jacobson, as would appear from the loss of the prevomer.

In the Cynodonts, the septomaxillary is always present. In the lower types it appears on the face, but in the higher forms it is almost entirely inside the nostril.

Among Mammals a septomaxillary is known only in some of the lower forms. In *Tritylodon* it appears on the face between the nasal and premaxillary, in much the same way as in *Nythosaurus*. In *Ornithorhynchus* and *Echidna* it would appear from the researches of Gaupp that what used to be regarded as the upper part of the premaxillary is really the septomaxillary. If this be so, as seems pretty certain, then the Monotremes have the septomaxillaries better developed than in the Cynodonts.

The only higher mammal in which there is a bone to be regarded as probably the septomaxillary is *Dasypus*. Here a small bone, which I described in 1897 as the "nasal-floor bone" and suggested might be homologous with the upper part of the premaxillary in the Monotreme, is probably to be regarded as a rudimentary septomaxillary.

Vomer and *Prevomers.*

In 1895, and more fully in 1902, I showed that there was reason to believe that the so-called reptilian "vomers" were not homologous with the mammalian vomer, but that being formed as splints to the paraseptal cartilages in close association with the organs of Jacobson, they were really homologous with the bones that unite to form the "dumb-bell bone" of *Ornithorhynchus*; and that the mammalian vomer had its homologue in the so-called "parasphenoid" of the lower forms. As a new name was necessary for the reptilian "vomers," I proposed the name *prevomer*.

In the Batrachia we find all three bones well developed, the median true vomer or parasphenoid being especially large to support the base of the skull. When in the earliest true Reptiles the pterygoids came together, there was little need for the median vomer and it became greatly reduced. In the Cotylosaurian *Diadectes* the median vomer is still a fairly strong rod, but in the later Cotylosaurians or primitive Diapsidans *Pariotichus* and *Procolophon* the vomer is a very short pointed process. In most later Diapsidans the vomer remains a small unimportant element. It developes to a fair size in the Ophidia and becomes large and much specialised in the Chelonia. The prevomers, on the other hand, remain large in most Diapsidans, but where, as in the Chelonians and Crocodilians, the organs of Jacobson become much reduced or lost the prevomers likewise tend to disappear.

In the mammal-like Reptiles the vomer shows great variations. In the Therocephalians it is small as in the primitive Diapsidans, but with the development of a secondary palate a new function is given to it, and it becomes large. In the Anomodonts, though the secondary palate is only imperfectly formed, the vomer is large and extends well forward. In the Cynodonts, where the secondary palate is complete, the vomer is very large and extends from the basisphenoid to near the front of the snout. The front part of the bone corresponds so exactly in its relations to the mammalian vomer, that it is impossible to doubt that the bones are homologous. On the other hand, if the anterior part of the bone were lost it is probable that every one would agree, from the relations of the back part, that it was the homologue of the reptilian so-called "parasphenoid." In Mammals the vomer varies greatly in size. It is relatively very large in the Cetacea, sometimes extending from the basioccipital to the front of the rostrum, while in the Rodentia it is often more or less rudimentary.

The prevomers are large in the Dinocephalians and Therocephalians. In the Anomodonts they have completely disappeared. In the Cynodonts, with the formation of the secondary palate they are either greatly reduced (*Gomphognathus*) or quite absent (*Bauria*). In Mammals the prevomers are usually absent, their function as supports to Jacobson's cartilages being taken by the palatine processes of the premaxillæ. In only two mammals are they known for certain to occur as distinct bones, viz. *Ornithorhynchus* and *Miniopterus*, and in both of these the pair of bones fuse together to form a median bone before the animal is full-grown.

Some observations have recently been made which at first sight appear to cast a little doubt on the homology of the parasphenoid with the mammalian vomer.

Versluys has discovered what he believes to be a large parasphenoid in *Dermochelys* in addition to the vomer and in no way connected with it. If this determination be correct, it will probably turn out that the Chelonian vomer is after all a pair of prevomers fused. The early development of the Chelonian vomer has not, so far as I am aware, ever been examined, and in my paper on the reptilian and mammalian vomerine bones I spoke very guardedly on the subject. So far as we know, the Chelonian vomer is always a median unpaired bone. But if it be a true vomer, what of Versluys' supposed parasphenoid? Fuchs has shown that in *Chelone* the basisphenoid is ossified by a large irregular exostosis on its under side, and that this exostosis bears relations to the pterygoids very similar to those which the parasphenoid of Versluys does. In the light of the observations of Fuchs, I think it must be concluded that the supposed parasphenoid in *Dermochelys* is entirely a development of the basisphenoid, and not the homologue of the parasphenoid of other reptiles.

Gaupp and Fuchs have both apparently discovered a rudimentary ossification behind the vomer in Chelonians which they believe to be a true parasphenoid, and Fuchs has discovered what he believes to be a rudimentary parasphenoid in *Didelphys*. The situation of these rudimentary ossifications is undoubtedly that of the parasphenoid, but they are also in the region normally occupied by the vomer in Mammals. When a bone which occupies one region in an ancestor comes to occupy a somewhat different region in a descendant through a portion of the bone becoming aborted, it is by no means uncommon that rudimentary ossifications can be detected in the region abandoned. The os carunculæ is undoubtedly the internasal process of the premaxilla in *Ornithorhynchus* and *Echidna*, but though it is quite detached from the premaxilla, it is nevertheless a portion of the premaxilla. In the case of the vomer, supernumerary ossifications appear to be not uncommon both in front and behind. In *Orycteropus* there are two small ossifications in front, apparently not prevomers, but detached ossifications of the true vomer. Kitchen Parker seems to have found them so commonly present that in some groups he regarded them as the rule. Speaking of the condition in Marsupials he says: "The main vomer is often relatively small; there is, nearly always, a pair of antero-lateral vomers . . . . and large postero-lateral, and other, or postero-medial vomers; these are very irregular and unsymmetrical in the young *Cuscus* especially, in which I find *ten* vomerine bones." Parker's postero-medial vomers are probably the ossifications regarded by Fuchs as parasphenoids, and there seems no reason to regard them as of any more morphological significance than the Wormian bones in the human skull.

Alisphenoid.

Until recently the alisphenoid bone has been looked upon, like the orbito-sphenoid, as an ossification of the cranial wall, and according to Parker "the alisphenoids and orbito-sphenoids appear as chondrifications of the walls of the skull." In studying the development of the marsupial skull some years ago, I found that the alisphenoid has originally nothing to do with the walls of the skull. It first appears as a short rounded rod lying outside the trabecula and quite independent of it or of any other skeletal structure. In its relations it seems exactly to correspond to the middle part of the cartilaginous bar on which the pterygoid bone develops in Lizards and *Sphenodon*. In the majority of Lizards this middle part gives rise to the epipterygoid or columella cranii. When, as in *Chamæleon*, the epipterygoid is rudimentary, the short bar which forms its base is almost exactly similar in structure and relations to the bar from which the alisphenoid developes in Mammals. One therefore seems driven to the conclusion that the epipterygoid and the alisphenoid are different developments of the same element. And this conclusion seems borne out by comparative anatomy, for we find that most Reptiles have either an epipterygoid or an alisphenoid, but never both. In Lizards we find an epipterygoid, but never an alisphenoid: in Snakes an alisphenoid, but never an epipterygoid.

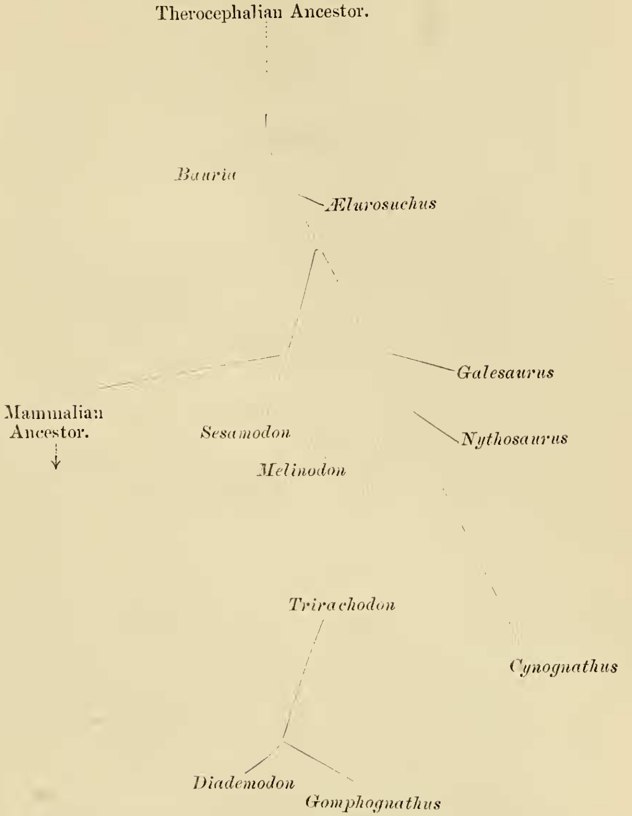
There seems little doubt that the epipterygoid is the early type of development. We find, for example, in the primitive *Procolophon* a columella cranii almost exactly like that of the lizard. In the Therocephalians the columellæ are long and slender, but usually flattened. In the Anomodonts they are slender, but rounded. In the Cynodonts we find no longer the columella cranii, but in its place a broad fan-shaped alisphenoid. The Cynodont alisphenoid further differs from the columella cranii of the earlier forms in having the lower part well developed and replacing the backward extension of the pterygoid. In the mammal the alisphenoid differs from that of the Cynodont mainly in having the 2nd and 3rd branches of nerve v. passing through it instead of behind it.

[*Note by* EDITOR.—In Dr. Broom's memoir as presented to the Society there followed here a discussion of the quadrate and tympanic, illustrated by two diagrams. A recent discovery made by Dr. Broom has considerably modified his views, and he has asked leave to withdraw the paragraphs omitted here until he has time to work out and present to the Society in a fuller form the bearings of his new facts.—*August* 11th, 1911.]

Angular.

The angular is found in all mammal-like reptiles. It is large in the Dinocephalians, Anomodonts, and Therocephalians, but comparatively small in the Cynodonts. In Mammals there is a small splint-bone on the lower side of Meckel's cartilage which is probably the remains of the angular. In *Ornithorhynchus* there appear to be two splint-bones, one being probably the surangular.

In the following diagram is represented what appears to be the genetic relationships of the principal known Cynodont genera :—



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Explanation of lettering in the Plate and Text-figures.

Ang. Angular; *Art.* Articular; *Aud.gr.* Auditory groove; *B.O.* Basioccipital; *B.S.* Basisphenoid; *Dent.* Dentary; *E.O.* Exoccipital; *Ex.st.* Extrastapedial; *Fr.* Frontal; *Ju.* Jugal; *I.P.* Interparietal; *La.* Lachrymal; *Mall.* Malleus; *Men.* Meniscus; *Mx.* Maxilla; *Na.* Nasal; *O.O.* Opisthotic; *Pa.* Parietal; *Pal.* Palatine; *Pmx.* Premaxilla; *Po.O.* Postorbital; *Pr.F.* Prefrontal; *Pt.* Pterygoid; *P.Vo.* Prevomer; *Qu.* Quadrate; *S.Ang.* Surangular; *Smx.* Septomaxillary; *S.O.* Supraoccipital; *Sq.* Squamosal; *Tym.* Tympanic; *Vo.* Vomer.

EXPLANATION OF PLATE XLVI.

Fig. 1. Side view of the cranial wall of *Cynognathus berryi.* Half nat. size.
2. Occiput of *Cynognathus berryi.* Half nat. size.
3. Side view of the skull of *Melinodon simus.* Nat. size. This represents the type and only known specimen. It is so badly crushed that it is impossible to restore it with any confidence. Six molars of the right side are preserved, and the axes of two molar series make with each other an angle of about 60°. The frontal region is certainly narrow, and as the teeth are very similar to those of *Sesamodon* it is probable that the skull is also somewhat similar, but probably the snout is shorter in *Melinodon* and the skull relatively broader.
4. The molar teeth of the left side of *Sesamodon browni* as preserved. × $1\frac{1}{2}$.
5. Base of the skull of *Sesamodon browni* as preserved. × $1\frac{1}{2}$.
6. Quadrate and part of the squamosal of *Bauria cynops,* as seen from the front. Nearly twice nat. size.
7. Base of skull of *Bauria cynops,* viewed partly from the side to show the deep keel of the basisphenoid.
8. Occiput and base of skull of *Bauria cynops,* viewed from behind and partly from below. Slightly restored. About two-thirds nat. size.
9. Median section of skull of *Diademodon.* All parts in unbroken line are from the specimen in the South African Museum. The prevomer and septomaxillary as restored are founded partly on the British Museum specimen of *Gomphognathus* and are partly hypothetical, the inner part of neither bone being known in any specimen. About half nat. size.